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The systematic status of Australian Strongyloidea (Nematoda)

by Ian Beveridge

Abstract. — The systematic relationships of the genera of Strongyloidea present in Australian marsupials are reviewed. The hypothesis that these genera are monophyletic is presented, based on characters of the dorsal ray and spicule sheaths, and the family Cloacinidae Travassos, 1919, is resurrected for them. Two subfamilies are admitted, Cloacininae and Phascolostrongylinae Lichtenfels, 1980, with the latter being subdivided into three tribes, Phascolostrongylinea (Lichtenfels, 1980 subf.), Hypodontinea trib. nov. and Macropostrongyloidinea trib. nov. The phylogeny of the family Cloacinidae is discussed, as well as its relationship with other families of the Strongyloidea.

Résumé. — Les relations systématiques entre les différents genres des strongles parasites de marsupiaux australiens sont réexaminées. L'ensemble de ces genres, rassemblés dans la famille des Cloacinidae Travassos, 1919, qui est revalidée, pourrait être considéré comme un groupe monophylétique : cette hypothèse s'appuie sur l'étude des caractères de la bourse caudale et sur ceux des gaines des spicules. Deux sous-familles sont admises : les Clocininae et les Phascolostrongylinae Lichtenfels, 1980. Cette dernière est à son tour subdivisée en trois tribus : les Phascolostrongylinea (Lichtenfels, 1980, s. fam.), les Hypodontinea trib. nov. et les Macrospostrongyloidinea trib. nov. La phylogénie de la famille des Cloacinidae et les relations de celles-ci avec d'autres familles de Strongyloidea sont discutées.

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Among the most prominent parasites of large herbivorous Australian marsupials are the genera of the nematode superfamily Strongyloidea, which occur in the stomach, oesophagus and large intestine of kangaroos and wallabies as well as in the large intestine of wombats. At present some 40 genera are known but many species still await description. The most recent review of the systematics of the Strongyloidea is that of Lichtenfels (1980), however some 15 new genera and two new tribes have since been described (Beveridge, 1981*a, b*, 1982*b*, 1983, 1986*b* ; Beveridge and Johnson, 1981 ; Mawson, 1979 ; Smales, 1982*a, b*).

In the classification of Lichtenfels (1980) (fig. 4A), strongyloid genera from Australian marsupials were distributed between two families, Chabertiidae (Popova, 1952) and Strongylidae Baird, 1853, the distinction between them being based primarily upon the structure of the ovejector and secondarily upon the number of branches of the dorsal ray. Australian genera within the Chabertiidae, except *Corollostrongylus* Beveridge, 1978*b*, were placed in a single subfamily, the Cloacininae, characterised by the lack of a cervical collar, the origin of the externodorsal ray close to the lateral rays and the presence of two pairs of dorsal ray branches. This subfamily united for the first time a variety of genera, parasitic in the stomachs and oesophagi of macropodid marsupials, which had hitherto been distributed between the Cloacinidae Travassos, 1919, and Trichonematidae Witenberg, 1925. *Corollostrongylus* was placed in the related subfamily Chabertiinae Popova, 1952, because of the presence of a globular buccal capsule and a Type II or J-shaped ovejector.

Within the Strongylidae, *Hypodontus* Moennig, 1926, and *Macropicola* Mawson, 1978*b*, were placed in the subfamily Strongylinae because both possessed globular buccal capsules and Type I or Y-shaped ovejectors, while a new subfamily, the Phascolostrongylinae Lichtenfels, 1980, was created for the genera *Phascolostrongylus* Canavan, 1931, *Oesophagostomoides* Schwartz, 1928, *Macropostrongyloides* Yamaguti, 1961, and *Paramacropostrongylus* Johnston and Mawson, 1940, characterised by a cylindrical buccal capsule, the presence of a dorsal gutter, and a Type I ovejector. The strongyloid genera present in Australian marsupials were therefore conceived of as polyphyletic in origin, and distributed among four subfamilies of the Strongyloidea.

Beveridge (1982*a*) by contrast suggested that the Australian strongyloids might be monophyletic in origin, basing his suggestion on the fact that all had similar dorsal rays and associated male genital structures, together with the fact that transitional forms of ovejector and buccal capsule were present linking nematode genera with the typical Type I and Type II ovejectors in the first case, and with globular and cylindrical buccal capsules in the second. Details of the hypothesis were presented very briefly.

In this paper the principal morphological features of Australian strongyloids are described and compared with related groups from other continents. Their classification is re-examined and the possible phylogenetic implications of the observations are discussed in relationship to the hypothesis presented earlier in out-line (Beveridge, 1982*a*).

MORPHOLOGICAL FEATURES OF AUSTRALIAN STRONGYLOIDEA AND COMPARISONS WITH TAXA FROM OTHER CONTINENTS

1. **Buccal capsule**

CLOACININAE

In all genera of the Cloacininae, the buccal capsule is relatively small and cylindrical in form. A dorsal gutter is lacking, and in species where the dorsal oesophageal gland has been observed, it opens to the buccal capsule on a slight eminence situated on the dorsal sector of the oesophagus (Beveridge, 1979*a*).

PHASCOLOSTRONGYLINAE

Phascolostrongylus and *Oesophagostomoides* both possess large cylindrical buccal capsules (fig. 1 D). A prominent dorsal gutter is present, and it terminates near the anterior

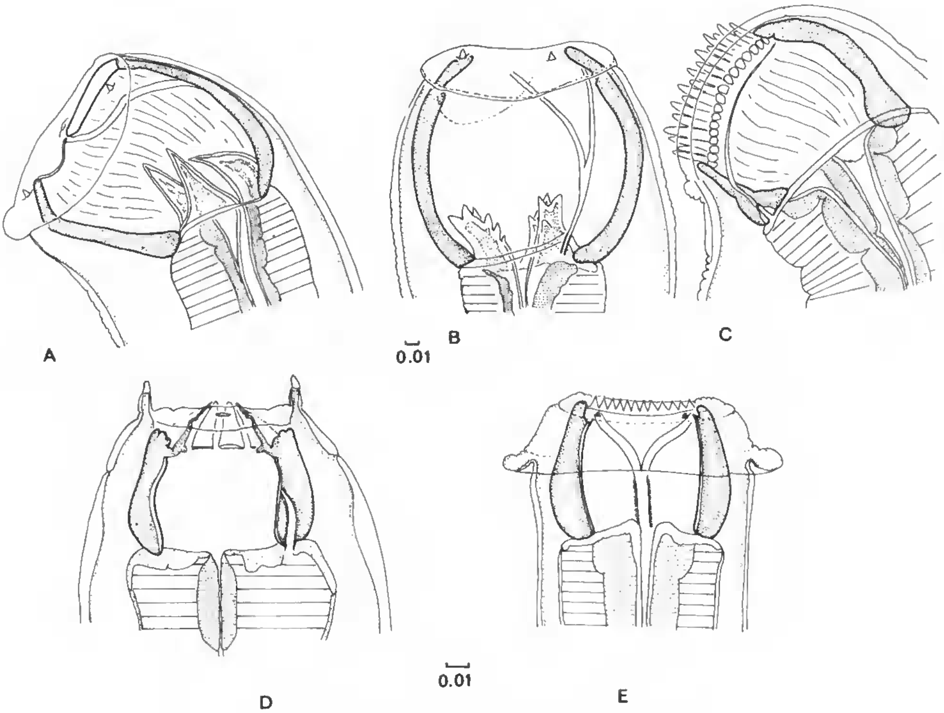

FIG. 1. — Buccal capsules of Australian Strongyloidea.

A, *Hypodontus macropi* Moennig, 1929, lateral view, note globular nature of capsule with oesophageal teeth and dorsal gutter. B, *Macropicola ocydromi* Mawson, 1978 ; note globular, undeviated buccal capsule with oesophageal teeth and Y-shaped dorsal gutter. C, *Corollostrongylus hypsiprymnodontis* Beveridge, 1978, lateral view ; note globular nature of buccal capsule, oesophageal teeth and leaf crowns. D, *Oesophagostomoides stirtoni* (Mawson, 1955), lateral view ; note large, almost cylindrical buccal capsule, leaf crowns and dorsal gutter within wall of buccal capsule. E, *Paramacropostrongylus toraliformis* Beveridge and Mawson, 1978, dorsal view ; note large, almost cylindrical buccal capsule, Y-shaped dorsal gutter and denticles around mouth opening. (Scale line : 0.01 mm.)

extremity in a circum-oral groove (BEVERIDGE, 1978*a*). The buccal capsule of *Macropostrongyloides* and *Paramacropostrongylus* (fig. 1 E) is cylindrical and a dorsal gutter is present. In all species, the gutter runs anteriorly within the dorsal wall of the buccal capsule to about mid-length, before dividing into two arcuate branches running around the internal surface of the buccal capsule, and meeting ventrally. Viewed from the dorsal surface, the gutter has a characteristic Y-shape (fig. 1 E) (BEVERIDGE and MAWSON, 1978).

STRONGYLINAE

The genera *Hypodontus* and *Macropicola* possess large, globular buccal capsules with prominent dorsal gutters (fig. 1 A, B). The buccal capsule in *Macropicola* is symmetrical and is undeviated (MAWSON, 1978*b*), while that of *Hypodontus* is directed ventrally (BEVERIDGE, 1979*b*). Both possess the characteristic Y-shaped dorsal gutter described above for *Macropostrongyloides*. In both genera the gutter opens to the lumen almost from the base of the buccal capsule, and this contrasts with *Strongylus* spp. in which the gutter opens to the lumen only at the anterior end of the buccal capsule (GIBBONS, 1984). Both genera lack the double leaf crowns that characterise the majority of the remaining strongyline genera.

CHABERTIINAE

Corollostrongylus has a large, globular buccal capsule which is dorsally deviated and because of this the dorsal gutter is very short and difficult to observe (fig. 1 C). It appears to be Y-shaped (BEVERIDGE, 1978*b*), and is thus similar to *Hypodontus* and *Macropicola*.

COMPARISONS WITH NON AUSTRALIAN GENERA

Among the Cyathostominae, the buccal capsule is cylindrical and the dorsal gutter opens at the anterior end. Species of *Poteriostomum* Quiel, 1919, and *Cylicostephanus* Ihle, 1922, have a division in the dorsal gutter before it reaches the anterior extremity of the buccal capsule, giving a gutter with a very slight Y-shape. Unfortunately, SEM studies on the dorsal gutters of cyathostomes have not been carried out, so that detailed comparisons with these genera cannot be made. BEVERIDGE (1979*b*) compared the Y-shaped dorsal gutter of *Hypodontus* with that shown in figures of the original description of *Castorstrongylus* Chapin, 1925. Examination of specimens of the latter genus in the (US National Helminth Collection no. 66368) indicates that the dorsal gutter in fact divides close to the anterior margin of the buccal capsule and is not Y-shaped as shown in the original figures of CHAPIN (1925). Prominently Y-shaped dorsal gutters are therefore restricted to Australian genera.

PHYLOGENY

LICHTENFELS (1980) considered that in both the Chabertiidae and the Strongylidae, evolution of the buccal capsule had occurred in the same direction, from large globular buccal capsules to small cylindrical ones, and a similar series is evident in the Australian genera alone, from the globular buccal capsules of *Hypodontus, Macropicola* and *Corollostrongylus*, to the cylindrical, sometimes large buccal capsules, still provided with a dorsal gutter in the Phascolostrongylinae, and finally to the small cylindrical buccal capsules of the Cloacininae in which a dorsal gutter is absent. The Y-shaped dorsal gutter provides a link between *Hypodontus, Macropicola* (Strongylinae) and the Phascolostrongylinae.

2. **Bursa**

The bursae of Australian strongyloids are extremely uniform and are similar to genera of the Chabertiinae and Oesophagostominae Railliet, 1916. The dorsal lobe is as long as or only slightly longer than the lateral lobes, and the dorsal ray has two pairs of branches. *Phascolostrongylus turleyi* Canavan, 1931, may have additional vestigial branches present, though their size and shape is highly varaible (BEVERIDGE, 1978*a*). *Oesophagostomoides* *stirtoni* (Mawson, 1955) and *O. longispicularis* Beveridge, 1978*a* may have notches in the final branches of the dorsal ray which could also be considered as vestigial tertiary branches. The externodorsal ray arises with the lateral rays in the Cloacininae, but from the dorsal ray in all the Phascolostrongylinae and in *Hypodontus, Macropicola* and *Corollostrongylus*. The ventral rays are apposed, and the externolateral is normally shorter than and divergent from the other lateral rays.

3. **Genital cone**

The genital cone has been relatively well studied in the Trichostrongyloidea (Gibbons and Khalil, 1983) and its structure incorporated into classifications. The same is not true of the Strongyloidea where the comparative morphology of the genital cone has received scant attention. Chabaud and Rousselot (1956) and Chabaud (1957) gave details of the genital cones of strongyloid nematodes from elephants, and those of the genus *Strongylus* have been studied using scanning electron microscopy (Gibbons, 1984). In Australian Strongyloidea, the genital cone has been used as a taxonomic character at the species level (Beveridge, 1982*b*, 1983 ; Mawson, 1978*a*), but no encompassing study has been made.

In the strongyloids of Australian marsupials, the basic structure of the genital cone is uniform. The anterior or ventral lip of the cone is large and conical, generally extending to the edge of the bursa and bearing a prominent papilla at its apex. The posterior or dorsal lip is invariably much smaller and consists of a base which is reniform in apical view, and from which project two elongate, distally bifid structures bearing papillae (no. 7) at their apices. Depending upon the species, the dorsal lip may be additionally ornamented with projections between the pair of major projections or dorsal to them. The most elaborate appendages occur in the genus *Thylostrongylus* where they form a set of digitate processes arranged in the same pattern as the rays of the bursa (Beveridge, 1982*b*), and in *Macroponema* and in *Macropostrongyloides* which possess a fringe of fingerlike projections around the dorsal lip of the cone (Mawson, 1978*a* ; Beveridge and Mawson, 1978).

The genital cone of the marsupial strongyloids was compared with genera from other host groups. Representatives of genera examined were : Strongylidae : *Murshidia* Lane, 1914, *Quilonia* Lane, 1914, *Triodontophorus* Looss, 1902, *Cylicocyclus* Ihle, 1922 ; Chabertiidae : *Oesophagostomum (Bosicola)* Railliet and Henry, 1913 ; *Oesophagostomum (Proteracrum)* Railliet and Henry, 1913 ; *Daubneyia* Le Roux, 1940, *Chabertia* Railliet and Henry, 1909, *Bourgelatia* Railliet, Henry and Bauche, 1919, *Castorstrongylus* Chapin, 1925 and *Ransomus* Hall, 1916.

Two forms of genital cone were noted. In all genera from the Strongylidae, the dorsal lip of the cone is much larger than the ventral lip, is rectangular at the tip in apical view, is supported frequently by a large and complex extension of the gubernaculum into the dorsal lip, and the paired papillae (7) are inconspicuous but situated very close to the cloaca (fig. 2 A). The ventral lip is extremely small in comparison, is conical in shape, and has a papilla (0) at its tip (fig. 2 B).

In the Chabertiidae generally, the genital cone is less conspicuous, the ventral lip is conical (fig. 2 F), with the dorsal lip slightly longer than the ventral lip (except in *Bourgelatia*) (fig. 2 E) and bearing two large rounded but undivided projections for the papillae (7).

The gubernaculum (if present) is simple and is restricted to the body of the nematode rather than extending into the dorsal lip of the genital cone, as is the case in the Strongylidae. In *Castorstrongylus* and *Ransomus* both lips are larger than in other genera, but the same basic structure exists.

The structure of the genital cone appears therefore to parallel the number of branches of the dorsal ray in separating the Strongylidae from the Chabertiidae, and further supports the use of this taxonomic character used initially by LICHTENFELS (1980).

The Australian strongyloids, on the basis of genital cone characters, are more similar to the Chabertiidae rather than the Strongylidae. Generally the Chabertiidae have a relatively short ventral lip, compared with the dorsal lip while the reverse is true in the Australian genera. *Bourgelatia* appears to be an exception. Similarly, the projections on the dorsal lip of the cone are bifid in Australian strongyles (except *Hypodontus*), but are undivided in the Chabertiidae studied. Some caution is needed however in drawing broad conclusions as the genital cones of strongyloids generally have been relatively little studied. Differences discussed above do suggest that they merit more detailed comparative study.

4. **Spicule sheaths**

BEVERIDGE (1982*b*) described and illustrated paired, elongate lateral thickenings and a central cordate thickening at the junction of the two spicule sheaths (fig. 2 J). It was noted that the cordate thickening had frequently been mistaken for a gubernaculum in the past, although a true gubernaculum was present in addition in certain species, but that the thickenings were present in all species of the Pharyngostrongylinea. These observations were subsequently extended to the Zoniolaiminea (BEVERIDGE, 1983). Similar thickened structures occur in all genera and species of the Cloacininae thus far examined.

Identical structures were described in *Hypodontus macropi*, though the significance of similarities with the Cloacininae was not realised at the time (BEVERIDGE, 1979*b*). Similar thickenings have been found in *Macrospostrongyloides, Paramacropostrongylus* (fig. 2 J), *Oesophagostomoides, Phascolostrongylus*, as well as in *Macropicola* and *Corollostrongylus*. All Australian genera of the Strongyloidea therefore possess this feature.

FIG. 2. — Bursa and associated genital structures of Strongyloidea depicting the major differences seen between families.

A, *Triodontophorus serratus* (Looss, 1900), lateral view of bursa, and genital cone showing complex gubernaculum, with extension of the gubernaculum into the dorsal lip of the cone. B, *T. serratus*, ventral view of genital cone, showing two components. C, *Quilonia africana* Lane, 1921, lateral view of bursa, showing 3 pairs of dorsal ray branches and large dorsal lip of genital cone. D, *Chapiniella larensis* Diaz-Ungria and Gallardo, 1968, ventral view of gubernaculum, note similarity of structure with that found in *T. serratus* (B). E, *Bourgelatia pricei* (Schwartz, 1928), lateral view of bursa, showing large ventral lip to genital cone and simple gubernaculum. F, *Chabertia ovina* (Fabricius, 1788), lateral view of bursa, showing gubernaculum and genital cone. G, *C. ovina*, dorsal view of dorsal lip of genital cone, showing undivided projections bearing nerve endings. H, *Codiostomum struthionis* (Horst, 1885), ventral view of bursa, showing dorsal ray and gubernaculum. I, *C. struthionis*, lateral view of genital cone. J, *Paramacropostrongylus typicus* Johnston and Mawson, 1940, ventral view showing simple gubernaculum posterior to cordate and paired elongate and thickenings of spicule sheaths. K, *Deletrocephalus dimidiatus* Deising, 1851, ventral view of genital cone. L-M, *D. dimidiatus*, variation in dorsal ray branches. (Scale lines : 0.1 mm.)


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An examination of other Strongyloid genera for comparable structures revealed the following results. In the Strongylidae (except for Australian genera), comparable structures were absent. In the genera *Strongylus* Mueller, 1780, *Triodontophorus* Looss, 1902 (fig. 2 B) and *Chapiniella* Yamaguti, 1961 (fig. 2 D) a complex gubernaculum is present which performs a similar function to the spicule sheath thickenings. The complex gubernaculum has been described by Popova (1952, 1958) and Lichtenfels (1980). In the genus *Murshidia*, a simple gubernaculum is present, the spicule sheaths are extremely muscular and thickenings of the spicule sheaths are absent. By contrast, in the Chabertiidae, thickenings of the spicule sheaths identical to those found in Australian genera were present in *Agriostomum* Railliet, 1902 (Chabertiinae) and in *Oesophagostomum* Molin, 1861, *Bourgelatia* and *Daubneyia* (Oesophagostominae), but not in *Chabertia* itself. In addition, the structures are present in *Stephanurus* Diesing, 1839, and in *Deletrocephalus* Diesing, 1851. The spicules of *Syngamus* Siebold, 1836, are so reduced in size as to render the accessory spicular structures almost invisible. In *Codiostomum* Railliet and Henry, 1911 (fig. 2 H), a complex muscular structure is present at the junction of the spicule sheaths, but is different to the refractile thickenings seen in other genera.

In conclusion, thickenings of the spicule sheath are present in all genera examined (except *Chabertia*) with four dorsal ray branches, and are absent in all genera examined which possess six dorsal ray branches.

5. **Ovejector**

The presence of a Y-shaped (Type I) ovejector with elongate sphincters and vestibules is considered a primitive character within the Strongyloidea (Lichtenfels, 1980). A Y-shaped ovejector of this type occurs in the Australian genera *Phascolostrongylus, Oesophagostomoides, Hypodontus* and *Macropicola* (fig. 1 B, E) (Beveridge, 1978*a*, 1979*b* ; Beveridge and Mawson, 1978) although the sphincters are not always elongate.

Within the Cloacininae, the ovejector is characteristically J-shaped (fig. 3 D), the sphincters are short, the infundibula are similar in length to the sphincters, but the vagina vera is much longer than that associated with Y-shaped ovejectors. The J-shaped ovejector is considered an evolved character (Lichtenfels, 1980). Two exceptions exist in the Cloacininae. In *Macropostrongylus yorkei* Baylis, 1927 (fig. 3 C) and *M. macrostoma* Davey and Wood, 1930, the vagina vera is extremely short, the ovejector is more Y-shaped than

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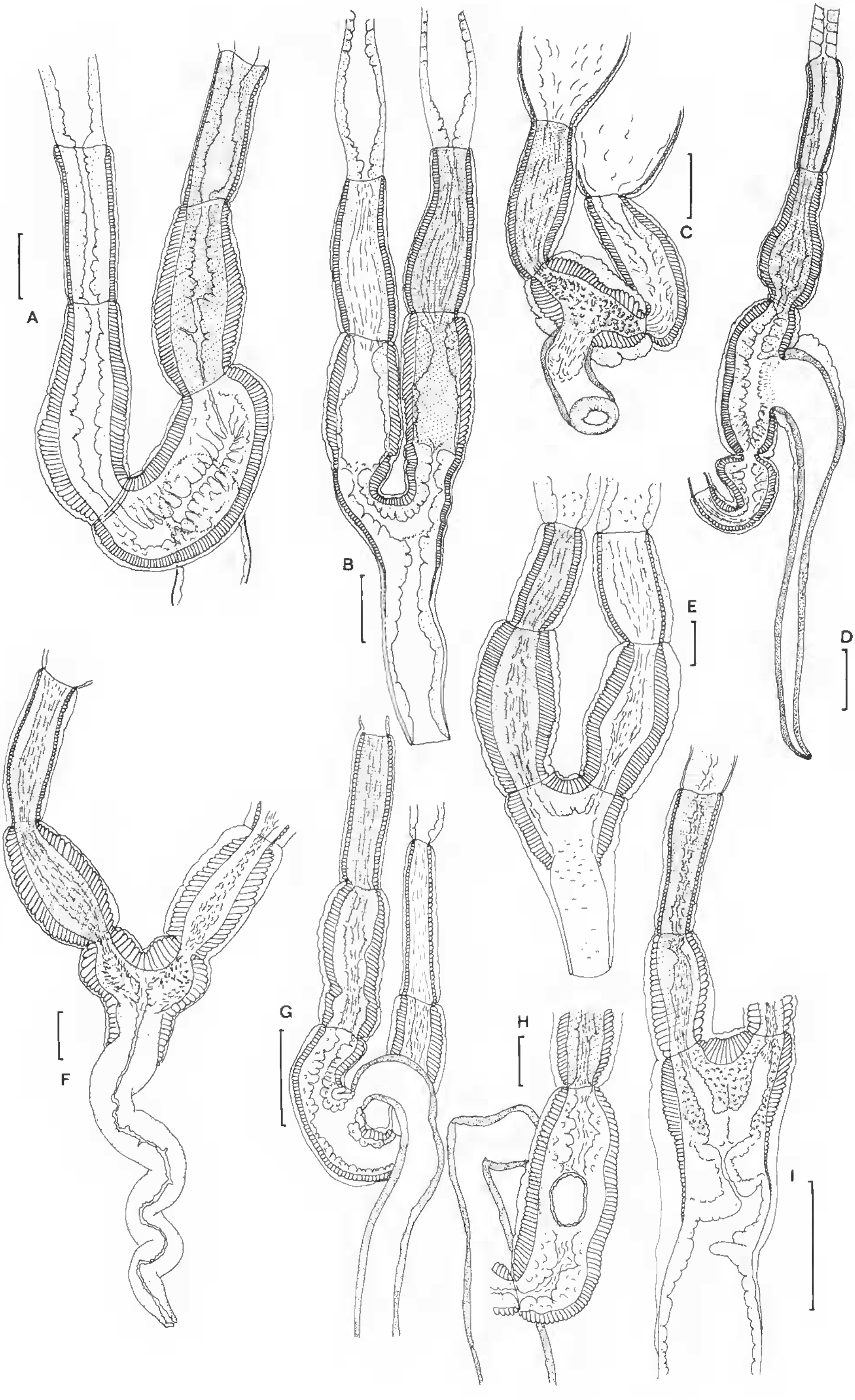
Fig. 3. — Ovejectors of Australian Strongyloidea, illustrating that although typical Type I and Type II ovejectors are present, so also are a variety of intermediate or atypical types.

A, *Macropostrongyloides dissimilis* ; intermediate ovejector with vestibule partly turned towards J position. B, *Oesophagostomoides stirtoni* ; typical Y-shaped or Type I ovejector. C, *Macropostrongylus yorkei* ; atypical Type II ovejector with short vagina vera, but well developed vestibule almost in Y position. D, *Macropostrongylus macropostrongylus* ; typical Type II or J-shaped ovejector. E, *Macropicola ocydromi* ; typical Type I ovejector. F, *Paramacropostrongylus toraliformis* ; modified Type I ovejector. G, *Corollostrongylus hypsiprymnodontis* ; atypical Type II ovejector, with vagina vera entering almost an anterior aspect of vestibule. H, *Paramacropostrongylus typicus* ; modified Type I ovejector, with vagina recurving before entering vestibule. I, *Woodwardstrongylus* sp. (undescribed). Atypical Type II ovejector. (Scale lines : 0.1 mm.)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J-shaped, but the vestibule is well developed aligning them with the Type II rather than Type I ovejectors (Beveridge, 1986*a*). Similarly, the ovejector of *Woodwardostrongylus* Wahid, 1964 (fig. 3 I) is more Y than J-shaped, but was correctly classed as a modified Type II ovejector by Lichtenfels (1980) because of the poor development of sphincters and infundibula. All Cloacininae therefore have a Type II or evolved ovejector.

The genera *Macropostrongyloides* and *Paramacropostrongylus* were identified as having a Type I ovejector by Lichtenfels (1980) but only in *M. lasiorhini* (Mawson, 1955), *M. baylisi* (Wood, 1930) and *M. yamagutii* Beveridge and Mawson, 1978 is the ovejector typical of this class. In *P. toraliformis* (fig. 3 F), the ovejector is Y-shaped and the sphincters are well developed, but the vagina vera is generally elongated. In *M. dissimilis* (Johnston and Mawson, 1939) (fig. 3 A) and in *P. typicus* Johnston and Mawson, 1940 (fig. 3 H), the vagina vera is long but the vestibule is turned almost into the J position. In parallel with this, the vestibule is larger than in typical Type I ovejectors but the sphincters are quite prominent. The ovejectors in these genera are therefore basically Type I, but include as well as typical forms, ovejectors tending towards Type II with elongation of the vagina vera, turning of the vestibule towards the J position, and enlargement of the vestibule. The presence of these intermediate forms of ovejector suggests that evolution of Type I and Type II ovejectors has occurred within the Phascolostrongylinae. It has therefore occurred twice in the entire Strongyloidea, since Lichtenfels (1980) identified a further series of intermediate ovejectors linking the Strongylinae with the Chabertiinae.

Corollostrongylus (fig. 3 G) has an ovejector which is basically Type II in form, since it has a long vagina vera, a well developed vestibule and is displaced from the typical Type I position. However, its displacement resembles that of *M. typicus* rather than that of a typical Type II ovejector, and the sphincters and infundibula are well developed. The ovejector in *Corollostrongylus* is intermediate in form between the two basic types, but has more features of a Type II ovejector, as noted by Lichtenfels (1980).

There is a correlation therefore between type of ovejector, origin of externo-dorsal rays and type of buccal capsule. Genera with large buccal capsules and with dorsal gutters have Type I or intermediate type ovejectors, while genera with small cylindrical buccal capsules and lacking dorsal gutters have Type II ovejectors. The former group has the externodorsal ray arising from the dorsal ray while in the latter group it arises separately.

6. **Third larval stage**

The buccal capsule of the third larval stage of *Rugopharynx rosemariae* Beveridge and Presidente, 1978, is formed from three sclerotised hook-like elements, with the hafts directed posteriorly (Beveridge and Presidente, 1978). Similar structures occur in *Labiostrongylus eugenii* (Johnston and Mawson, 1940) (Smales, 1977), in *L. bipapillosus* (Johnston and Mawson, 1939) and *Rugopharynx australis* (Moennig, 1926) (unpublished observations), and appear to be characteristic of the Cloacininae. Sclerotised thickenings of the buccal capsule occur in the third larval stage of *Hypodontus*, but are not hook-like in form (Beveridge, 1979*b*). The buccal capsule in the comparable larval stages of *Chabertia* and *Oesophagostomum* is cylindrical. Thus the third larval stages or Cloacininae appear to possess a unique buccal capsule morphology.

PHYLOGENETIC IMPLICATIONS

Lichtenfels (1980) divided the Chabertiidae from the Strongylidae primarily on the basis of the type of ovejector (fig. 4 A), considering the Y-shaped or Type I ovejector as primitive and the J-shaped or Type II ovejector as evolved. He noted a general correlation between ovejector shape and number of branches of the dorsal ray, with three pairs of branches being primitive and two pairs evolved. The only major exceptions to this pattern were the Australian genera belonging to the Phascolostrongylinae as well as *Hypodontus* and *Macropicola* which possess a Type I ovejector, but two pairs of branches to the dorsal ray (fig. 4 A). These exceptions are readily overcome if the number of dorsal ray branches is used as a primary character, and the ovejector accorded a secondary position. There are two reasons for making such a change. Within the Australian strongyloids, the type of ovejector is somewhat variable and in the Phascolostrongylinae there are transitional forms, making their precise classification difficult. The dorsal ray by contrast usually has either two or three pairs of branches, and is therefore easier to assess. Secondly, as described above, there is an excellent correlation in the Strongyloidea between the number of pairs of branches on the dorsal ray and the presence or absence of thickenings of the spicule sheath. If the latter two male characters are taken together, and the structure of the ovejector neglected for the time being, the basic structure of Lichtenfels' (1980) classification remains unaffected, except that the apparent anomaly of the Australian genera is resolved. In terms of Lichtenfels' (1980) proposed classification, Phascolostrongylinae, *Hypodontus* and *Macropicola* would be removed from the Strongylidae and placed in the Chabertiidae. Thus all the Australian genera would occur in a single family. In addition, the minor inconsistency of *Hypodontus* and *Macropicola*, without leaf crowns, in a subfamily (Strongylinae) in which double leaf crowns are usual, is overcome.

The Chabertiidae in Lichtenfels' classification contains three subfamilies, Chabertiinae and Oesophagostominae, parasitic principally in ungulates and rodents, and the Cloacininae parasitic in marsupials. The Phascolostrongylinae which is now added is readily distinguished from these three subfamilies since it alone possesses a Type I ovejector. *Hypodontus* and *Macropicola*, both of which possess a Type I ovejector, are therefore added to the Phascolostrongylinae. This transfer links together all of the Australian genera with the peculiar Y-shaped dorsal gutters in a single subfamily. The only remaining Australian genus, *Corollostrongylus*, was placed in the Chabertiinae by Lichtenfels (1980) because it possesses a large globular buccal capsule and what was interpreted as Type II ovejector. However, because of the presence of transitional ovejectors in *Macropostrongyloides*, that of *Corollostrongylus* may equally be interpreted as a similar transitional form. For this reason, *Corollostrongylus* is transferred, with some reservations, to the Phascolostrongylinae.

The revised arrangement implies therefore that the evolution of the ovejector from Type I to Type II has occurred either uniquely within the Australian genera, since obvious intermediate forms are present in the Phascolostrongylinae, or that it has occurred twice in parallel in the Strongyloidea, once in the Australian genera, and once elsewhere to give the Type II ovejectors found in the Chabertiinae and Oesophagostominae.

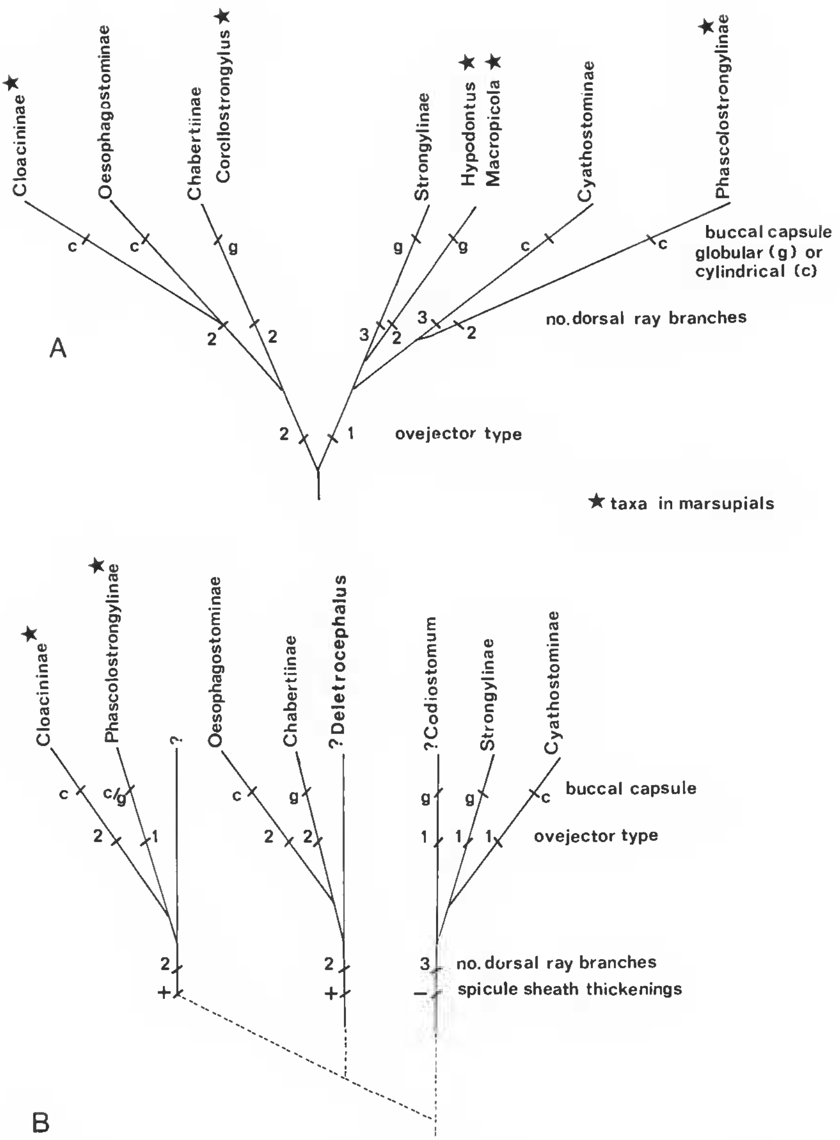

FIG. 4. — A, Cladogram of strongyloid taxa derived from LICHTENFELS (1980) ; those in marsupials (★) occur in four of the five subfamilies, inferring a polyphyletic origin. B, Alternative arrangment based primarily on male characters, the number of dorsal ray branches and the presence of spicule sheath thickenings, and using ovejector type and buccal capsule structure as secondary characters. Three groups emerge, with the taxa from marsupials grouped together.

The Chabertiidae (*sensu* LICHTENFELS, 1980) therefore contains four subfamilies, the Chabertiinae, Oesophagostominae, Cloacininae and Phascolostrongylinae. The Chabertiinae and Oesophagostominae are probably related (LICHTENFELS and PILITT, 1985). Both subfamilies usually possess pairs of leaf crowns, the primitive genera of the Chabertiinae with large globular buccal capsules probably gave rise to the small cylindrical or ring-shaped buccal capsules of the Oesophagostominae, and both subfamilies occur in ungulates and rodents with a few genera in primates. The Cloacininae and Phascolostrongylinae may be similarly related. There is an evolution from large and often globular buccal capsules to small cylindrical ring-like buccal capsules which correlates with the evolution of the ovejector from Type I to Type II, double leaf crowns are rare (present in three genera only) and if present, the nematodes have a Type I ovejector. The two subfamilies are both parasitic in marsupials. For this reason, two parallel lines of evolution are thought to have occured, namely Chabertiinae — Oesophagostominae and Phascolostrongylinae — Cloacininae. If this hypothesis is correct, then the latter lineage cannot adequately be accommodated within the Chabertiidae, and the family Cloacinidae Travassos, 1919, could be resurrected to contain Cloacininae and Phascolostrongylinae.

Relationships of genera within the reinstated Cloacinidae can be established (fig. 5) using the following criteria : (*a*) buccal capsule globular (plesiomorphic) or cylindrical (apo-

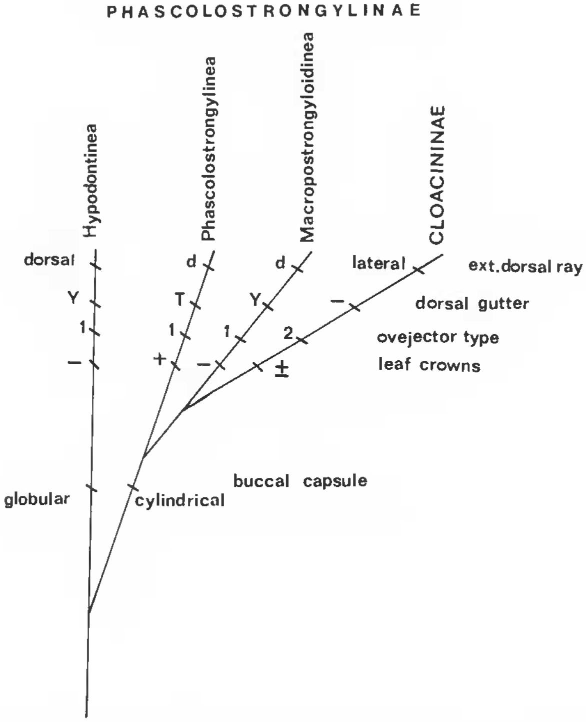

FIG. 5. — Cladogram depicting relationships of the Australian strongyloids derived by combining buccal capsule shape, presence of leaf crowns, ovejector type, presence of dorsal gutter and the original of the externo-dorsal ray.

morphic) ; (*b*) with (plesiomorphic) or without (apomorphic) dorsal gutter ; (*c*) and shape of dorsal gutter, Y-shaped being apomorphic.

Three groups of genera result, and each group has been placed in an independent tribe, thus making the subdivisions of the Phascolostrongylinae and Cloacininae comparable. *Hypodontus, Macropicola* and *Corollostrongylus* with globular buccal capsules are placed in the Hypodontinea trib. nov. ; *Phascolostrongylus* and *Oesophagostomoides*, with paired leaf crowns and a simple dorsal gutter are placed in the Phascolostrongylinea (Lichtenfels, 1980), while *Macropostrongyloides* and *Paramacropostrongylus* with denticles or teeth, no leaf crowns and a Y-shaped dorsal gutter are placed in the Macropostrongyloidinea trib. nov.

The revised arrangement of Cloacinidae is show below.

CORRELATION WITH HOST EVOLUTION

The phylogeny of the Australian taxa (fig. 5) conforms to some extent with the evolution of the hosts. The most primitive genera, in contrast to the hypothesis advanced by BEVERIDGE (1982*a*), are a related group (*Hypodontus, Macropicola* and *Corollostrongylus*) of monotypic genera with globular buccal capsules, Y-shaped dorsal gutters and with the mouth opening directed anteriorly, dorsally or ventrally, occurring in the large intestines of macropodids. *Corollostrongylus* occurs in *Hypsiprymmodon*, a small macropodid with a number of primitive morphological characters, while *Macropicola* in *Macropus fuliginosus* is probably a " capture " since the parasite, but not the host, is restricted to Western Australia (MAWSON, 1978*b* ; BEVERIDGE and ARUNDEL, 1979). *Hypodontus* occurs in a variety of macropodine hosts, but not in Potoroinae. The three genera may be relicts of an older radiation of parasites of the large intestine of macropodids. *Phascolostrongylus* and *Oesophagostomoides* with relatively large cylindrical buccal capsules occur in the colon of wombats, a family thought to have evolved in the Eocene (STIRTON *et al.*, 1968). They are similar to *Macrospostrongyloides* and *Paramacropostrongylus* and may represent a parallel lineage in a different host family.

Macropostrongyloides and *Paramacropostrongylus* are in some respects intermediate between the Hypodontinea and the Cloacininae. The buccal capsule has become reduced in some species to a small cylindrical form, but the Y-shaped dorsal gutter has been retained. The ovejector occurs in a variety of forms ranging from typically primitive Type 1 ovejectors to forms similar to the Type II found in Cloacininae. Some species are parasites of the large intestine of macropodids and vombatids, while others occur in the stomachs of macropodids. They therefore form a link between the caecum/colon inhabiting " primitive " genera and the " evolved " genera of the stomach and oesophagus. Macropodids such as *Hypsiprymmodon* are " primitive " to the extent that they are monogastric while in the remaining macropodids a sacculated stomach evolved and presumably opened up new niches for the Strongyloidea, which occur primarily in sites of fermentative digestion. *Macropostrongyloides* and *Paramacropostrongylus* may represent one of the first groups to have invaded the macropodid stomach and may be related to the ancestors of the Cloacininae. Within the stomachs of the Macropodinae, an explosive nematode radiation has occurred with some 33 genera described so far in the Cloacininae. A correlation therefore exists in part with the hosts, but more importantly with the evolution of the gastro-intestinal tracts of the herbivorous marsupials. The invasion of vombatids by certain genera from macropodids (*Macropostrongyloides*) is not parallel with host evolution, since vombatids pre-date macropodids in the fossil record.

ORIGINS

The hypothesis presented above on the relationships of the Australian Strongyloidea provides a plausible view of their evolution in marsupials but provides no clues at all as to their origins. The most primitive members of the Cloacinidae are more primitive (using LICHTENFELS' characters of the ovejector) than any of the Chabertiidae but are more specialised than the Strongylidae (based on bursal characters). This phyletic position does not lead to a simple zoogeographical hypothesis for their origins. The Australian Strongyloidea are restricted to the herbivorous diprotodont marsupials, and no nematode ancestors, understandably, are known from the carnivorous precursors of the diprotodonts. It seems reasonable therefore to assume that the diprotodonts acquired their strongyle parasites from some other herbivorous vertebrate group already established on the Australian continent. Of the strongyles occurring in host groups other than mammals, *Chapiniella* in reptiles can be eliminated as a possible ancestor since the hosts, land tortoises, are not known from the fossil record in Australia (GAFFNEY, 1981), and the genus *Chapiniella* is aligned to the Strongylidae by number of branches to the dorsal ray and the complex gubernaculum. Ratites (*Rhea, Struthio*) are parasitised by three primitive strongyloid genera *Deletrocephalus, Paradeletrocephalus* Freitas and Lent, 1947, and *Codiostomum* in South America and Africa, but none are known from Australian ratites, possibly due to the fact that parasites of ratites have not been examined in detail. The Cloacinidae is not derived obviously from any of the genera known in ratites, but the distribution of ratites on the southern continents, their antiquity and the presence of strongyloid genera in ratites on two of the continent's renders them promising candidates. The ratites have been important also in the evolutionary history of the Trichostrongyloidea (DURETTE-DESSET and CHABAUD, 1981). A third possibility that invading rodents might have carried strongyloid parasites to Australia with them from south east Asia and a transfer subsequently occurred to the marsupials is considered unlikely. No strongyloids are known currently from rodents in the Australasian region, while all of the strongyloids known from south east Asian rodents belong to the Oesophagostominae which would not be a suitable ancestral group. This latter hypothesis, if correct, would necessitate major changes in assumptions about the direction of morphological evolution in strongyloids. The possibility of an origin in ratite birds therefore remains most likely on the available evidence.

RELATIONSHIPS WITH OTHER STRONGYLOID FAMILIES

The characters utilised above in delineating the relationship of the Australian strongyloids can be applied to the remainder of the super-family Strongyloidea. Within the family Strongylidae, utilising the characters of the dorsal rays and spicule sheaths, two distinct groups are evident. First, all of the genera with the plesiomorphic characters of thick muscular spicule sheaths and three pairs of branches to the dorsal ray could be considered a single lineage. This would unite *Codiostomum* (Strongylinae) in ostriches, *Equinurbia* (Strongylinae), *Murshidia* and *Quilonia* (Quiloniinea) in elephants, tapirs, rhinoceros and warthogs, in a single lineage which is probably African in origin. All genera within this lineage have a Type I ovejector. A second major group united by a complex gubernaculum (assumed to be an apomorphic character) and three pairs of branches to the dorsal ray would be *Strongylus, Triodontophorus* (Strongylinae), and the Cyathostominea (Cyathostominae), all parasitic in equids. Again, all possess a Type I ovejector. The form of the genital cone and the dorsal ray unites this lineage with the first. The same combination of characters occur in *Chapiniella* (LICHTENFELS and STEWARD, 1981) in tortoises, though the buccal capsule is small and cylindrical. The parasites of tortoises may therefore be derived from the equid parasites if changes in the buccal capsule have followed other groups, or equally, may be ancestral to them, based on the female genitalia which are singularly primitive (LICHTENFELS and STEWARD, 1981). Apart from the genus in tortoises, therefore, two major groups within the Strongylidae emerge, one parasitic in equids and the other in proboscoids and perissodactyls, each presumably having a parallel evolution of globular to cylindrical buccal capsules. DVOINOS (1982, cited by LICHTENFELS, 1986) also concluded that the strongyloid parasites of equids are monophyletic.

By contrast, the presence of spicule sheath thickenings (considered to be apomorphic) together with two pairs of branches to the dorsal ray would link *Stephanurus*, Deletrocephalidae (in rheas), Chabertiidae and Cloacinidae. LICHTENFELS (1980) observed that the dorsal rays of *Deletrocephalus* and *Paradeletrocephalus* were variable in form. Examination of several specimens of *D. dimidiatus* Diesing, 1851 (USNMHC no. 66136) showed that the basic pattern was two pairs of dorsal ray branches with sometimes a third vestigial pair (fig. 1). The pattern is little different to that in the Phascolostrongylinea (BEVERIDGE, 1978*a*) which could theoretically share a common ancestor with the deletrocephalids because other features such as those of the buccal capsule (LICHTENFELS, 1980) could be used to argue that the strongyloid genera in ratites are more primitive than any occurring in mammals. The ovejector in deletrocephalids is Type I.

The plausibility of an association between cloacinids and deletrocephalids via an ancestor in Australian ratites has been considered briefly above. This hypothesis would require that the hypothetical Australian ancestor possess a dorsal ray with two pairs of branches, and a Type I ovejector, a situation which would accord readily both with the extant deletrocephalids and extant phascolostrongylines.

The position of the chabertiids within this scheme is more difficult to explain. If they are derived from the Strongylidae as suggested by LICHTENFELS (1980) then they have a series of morphological characters (four dorsal ray branches and spicule sheath thickenings) that they have developed in convergence with the cloacinids. If on the other hand, the chabertiids could be derived from the deletrocephalids (fig. 4 B), an association which is parsimonious in morphological terms may conflict with host zoogeography as the deletrocephalids are restricted to South America while the chabertiids are cosmopolitan (except in the Australasian region) in their distribution. Several mammal groups have migrated to the South American continent, but the only significant emigrants are the didelphoid marsupials (SARICH and CRONIN, 1980). This objection is not important if it is considered that the major divisions within the Strongyloidea occurred during the early Cretaceous (see LICHTENFELS, 1980), before the major period of continental separation. An essentially relict family in South American ratites and a cosmopolitan family of descendants would agree with the morphological evidence.

CONCLUSION

By combining the dorsal ray, spicule sheaths and genital cone, the strongyloids of mammals can be divided into three major groups, accorded family status here. The Cloacinidae in Australian marsupials could have evolved from an hypothetical ancestor in Australian ratites, related to deletrocephalids, and possessing a Type I ovejector, two pairs of dorsal ray branches, and spicule sheaths thickenings. The hypothesis that the Australian strongyloids originated from ratites (BEVERIDGE, 1982*a*) would be strengthened if the other major strongyloid lineages were associated with possible ancestor in ratites. The Strongylidae with a genus in African ratites appears to be such a possibility. The position of the chabertiids is uncertain, but they show some similarities with the deletrocephalids. LICHTENFELS' (1980) suggested that they arose from strongylid stock, a hypothesis which would require that similarities with the cloacinids are due to convergence.

The hypothesis that the Strongyloidea can be subdivided primarily according to the dorsal ray and the spicule sheaths remains to be tested against other characters. It does provide an explanation of the zoogeography of the Strongyloidea of Australian marsupials, but does not account fully for the relationships of the Chabertiidae, possibly because too few characters are still available for phylogenetic analysis, or possibly because the Strongyloidea is essentially a relict fauna, which many of the intermediate forms missing.

SYSTEMATIC STATUS OF AUSTRALIAN STRONGYLOIDEA

CLOACINIDAE (Stossich, 1899)

Strongyloidea. Dorsal ray with two pairs of branches ; accessory thickenings of spicule sheaths prominent ; ovejectors of Type I or Type II, transitional forms present ; double leaf crowns absent, or if present then in nematodes with Type 1 ovejector ; buccal capsule cylindrical or globular.

CLOACININAE Stossich, 1899

Cloacinidae. Ovejectors Type II. Buccal capsule cylindrical or ring-like ; small ; dorsal gutter absent ; externodorsal ray arises close to lateral trunk. Tribes : Cloacininea (Stossich, 1899), Macropostrongylinea Lichtenfels, 1980, Zoniolaiminea (Popova, 1952), Labiostrongylinea Beveridge, 1983, Pharyngostrongylinea Popova, 1952, Coronostrongylinea Beveridge, 1986.

PHASCOLOSTRONGYLINAE Lichtenfels, 1980

Cloacinidae. Ovejectors Type 1 or modified Type I ; buccal capsule cylindrical or globular ; dorsal gutter present ; externodorsal ray arises from dorsal ray.

PHASCOLOSTRONGYLINEA (Lichtenfels, 1980 subf.)

Ovejectors Type 1 ; buccal capsule large, cylindrical, straight ; dorsal gutter reaches anterior extremity of buccal capsule ; two leaf crowns present. Parasitic in Vombatidae (colon).

Genera : *Phascolostrongylus* Canavan, 1931 ; *Oesophagostomoides* Schwartz, 1928.

HYPODONTINEA trib. nov.

Ovejectors Type I or modified ; buccal capsule large, subglobular, directed anteriorly, dorsally or ventrally ; dorsal gutter Y-shaped ; oesophageal teeth or leaf crowns present. Parasitic in Macropodidae (caecum, colon).

Genera : *Hypodontus* Moennig, 1929 ; *Corollostrongylus* Beveridge, 1978 ; *Macropicola* Mawson, 1978.

MACROPOSTRONGYLOIDINEA trib. nov.

Ovejectors Type I or modified ; buccal capsule small, cylindrical, directed anteriorly, or slightly deviated ventrally ; dorsal gutter Y-shaped ; buccal capsule with teeth or denticles. Parasitic in Macropodidae (stomach, caecum), Vombatidae (colon).

Genera : *Macropostrongyloides* Yamaguti, 1961 ; *Paramacropostrongylus* Johnston and Mawson, 1940.

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